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Evolution and Human Behavior 31 (2010) 304–308

Evolution and Human Behavior

Book Reviews

Heavy hearts and heads held high — A review of *Glimpses of Creatures in Their Physical Worlds*

Steven Vogel. Princeton: Princeton University Press; 2009. 302 pp. $35.00

Glimpses of Creatures in Their Physical Worlds is a heart-pounding, heat-conducting, power-amplifying whirlwind tour through the mechanical and thermal worlds of Earth's living things. The journey has something for everyone: the thrills of explosively launched projectiles, the chills of supercooling polar fish, the rise of birds soaring on an ascending torus of ground-heated air. Along the way, there are insights into the functional analysis of biological systems, relevant not only to researchers in biomechanics but also to the broad community of scientists seeking to understand the workings of life's devices.

1. Amazing adaptations

The sandbox tree, or "monkey's pistol," shoots seeds 160 mph — 60% faster than the best pitchers can throw a baseball. An exploding fruit launches the 2-cm seeds up to 30 m. Vogel's foray into ballistics (chapter 2) begins with the standard idealized drag-free model in which the distance-maximizing launch angle is always 45°. He then explains how to estimate the range loss from drag, the "drag tax," for a projectile of a given speed, size, density and launch angle. For example, the seeds of the sandbox tree give a considerable drag tax of 94% (they would travel 500 m in a vacuum), which changes the optimal launch angle to about 30° — close to the mean of 34° observed for these seeds (Swaine & Beer, 1977). Vogel applies the model to several dozen projectiles from both biology (seeds, jumping bodies, etc.) and human artifacts (canon balls, golf balls, etc.). The analysis shows how increasing drag reduces the optimal launch angle. When drag is very high, some organisms, such as the fungus *Sordaria*, launch straight up to exploit wind-borne travel, maximizing rather than minimizing drag.

A tree frog launches its body with seven times more power than its muscles can directly produce (chapter 3). The trick is to store energy slowly and then suddenly release, like a crossbow or catapult. Vogel presents acceleration data for over 50 species ranging from tiny spores to jumping horses. He surveys a variety of power-amplifying devices. Grasshoppers use elastic storage to amplify their muscle power 40 times. Extensor muscles in the hind tibia load a pair of elastic elements, and they launch by releasing a catch near the knee joint. In the fungus *Sphaerobolus,* an osmotic engine builds pressure beneath the floor of a concave cup until it suddenly everts, propelling spores into the air.

The physics of heat creates problems and opportunities for organisms (chapters 4, 5 and 9). The silk tree regulates heat by varying its posture during the day, an African ground squirrel uses its tail for shade, and the antelope ground squirrel presses against burrow walls to cool by conduction. One thermal device is frequently put to use in both human technology and organisms: the countercurrent exchanger. In one variety, organisms conserve heat by arranging veins and arteries to facilitate heat transfer from outgoing arteries to incoming veins. This design has been found in many species, including the appendages of lemurs, anteaters, sloths, leatherback turtles, wading birds, and the tails of muskrats, beavers, and manatees. Vogel also discusses the problem of ice — the awkward fact that organisms contain a substance that crystallizes at temperatures that commonly occur. Some polar fish can keep water in a liquid state down to −10°C by "supercooling" in which they avoid substances that nucleate ice crystallization. Other organisms use protein-based antifreezes. Perhaps most impressive are creatures that tolerate partial freezing: 80% for periwinkle snails, 65% for some frogs, and 50% for many reptiles. In these organisms, specialized proteins initiate extracellular ice crystallization so it can be controlled. Also, their cell membranes need to withstand impinging crystals to protect against lethal intracellular ice.

Stress or cholesterol might drive a person's blood pressure over 140/90 mmHg, but a giraffe's resting blood pressure is double that — 280/180 mmHg. Chapters 6–8 address how gravity affects organisms in the air, on land, and underwater. For some creatures, gravity has important effects on the circulatory system, particularly when a critter's head is far above the heart. To hold their heads high, giraffes have a massive 25-lb heart, a heartbeat double our own, and specially reinforced blood vessels so they do not burst a pipe. Giraffes also have a series of one-way valves in the jugular vein so they can lower their heads without a sudden rush of blood. In snakes, the circulatory importance of gravity depends on behavior: Aquatic species feel little effect, whereas climbers often hold their heads far above their hearts. To deal with gravity, climbing snakes have higher blood pressure, reinforced vessels and hearts

1090-5138/$ – see front matter
doi:10.1016/j.evolhumbehav.2009.12.002

shifted further toward the head. Related issues arise in chapter 10 about pumps. Pounding hearts are not the only valve-and-chamber displacement pumps in nature; the same basic design powers the jet propulsion of squid and octopus. And there are a great variety of other pump designs including valveless chamber pumps in blood-sucking insects, piston pumps in some worms, moving chamber pumps like our intestines, osmotic pumps for launching fungus spores, and evaporative pumps that move water from soil to the leaves in terrestrial plants.

2. Overarching insights: focusing on functions

Vogel has more in mind than describing particular adaptations. Through examples, he is advocating a specific approach: "Instead of asking about the physical science behind a specific biological system, I'll consider an aspect of the physical world and ask what organisms, any organisms, make of it, both how they might capitalize on it and how they might be limited by it" (p. vii). The approach comes through crystal clear. Each chapter begins with models of physical phenomena such as diffusion, ballistics, gravity, heat transfer, or torsion. Next, Vogel often presents a dimensionless ratio or index that measures the relative effects of various physical factors for a given system, e.g., diffusion vs. convection (chapter 1), gravity vs. drag (chapter 2), or twistiness vs. bendiness (chapter 11). He then applies these tools to examine various biological devices and their alternative functional explanations. The framework offers a nuanced analysis of function, including the ability to distinguish the primary function of multifunctional mechanisms. For example, many aquatic animals use gills both for respiration and suspension feeding; estimating ratios of convective to diffusive transport of oxygen shows that the keyhole limpet's gills are primarily designed for respiration, whereas the mussel's gills are primarily designed for suspension feeding (chapter 1). In sum, Vogel sketches a physical phenomenon, describes the structure of relevant biological mechanisms, and then tests functional hypotheses by examining whether devices are improbably well organized to exploit a given effect or phenomenon (Williams, 1966).

The key characteristics of Vogel's approach can perhaps be clarified by considering what it does not include. First, there is no mention of genes. Vogel asserts that many important biological questions "require physical rather than chemical or genomic reduction" (p. viii). I might go further: from a functional perspective, genes are part of the *question* rather than the explanation. Genetic sequences are assembly machinery for organisms' devices, and they raise the same "problem of design" as eyes or pocket watches (Paley, 1828). The Darwinian answer to this question — why do complexly designed genes persist over time? — is given by the functions of the devices they assemble, which provide the relevant selective advantages. But when trying to understand anatomy, physiology or behavior, people seem drawn to look *inside* of organisms, e.g., to genes or some network of cells, perhaps because humans naturally think about organisms in terms of internal essences (Gelman, 2003; Shtulman & Schulz, 2008). Instead, the functions of devices are often best understood in terms of the environment *outside* of the organism, such as the principles that govern gravity, hydraulics, optics, computation, or, in social species, strategic interactions (e.g., DeScioli & Kurzban, 2007, 2009a,b). Second, the book has no measures of reproductive success. Although natural selection is based on reproduction rates, evolution produces devices with narrowly defined functions, as has been pointed out in psychology (Tooby & Cosmides, 1992). Hence, to test the function of grasshopper launch mechanisms, researchers proceed by focusing on a narrowly defined function — power amplification — rather than looking at reproduction rates. Third, there is no reliance on the fossil record. Questions about evolutionary function and evolutionary history are, well, different questions.

These distinctions between alternative approaches to biological systems might seem obvious to some, but they are not obvious to everyone. *Nature* recently published an essay titled "Can evolution explain how minds work?" (Bolhuis & Wynne, 2009), which aimed to discredit evolutionary approaches to human behavior. Embarrassing themselves (and *Nature*'s editors), the authors wrote that "the most serious problem with this perspective [evolutionary psychology] is that cognitive traits of past generations leave little trace in the fossil record" (p. 832). The critique is incorrect because the targeted researchers have long studied the evolutionary *functions* of cognitive systems, not their *histories*. But such a glaring mistake would fall flat if not for widespread confusion among naïve readers (and editors) about how scientists test hypotheses about evolved functions. Vogel's book shows with unmistakable clarity how to investigate the functions of biological mechanisms, including cognitive devices such as the vision-based control systems that continuously sense and stabilize the orientation of birds' bodies during flight (chapter 12) — no fossils necessary.

The insights and examples from *Glimpses of Creatures in Their Physical Worlds* can be used to help sharpen our understanding of biological functions and to better communicate these ideas to confused colleagues and pondering students.

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The psychologic gambit declined—a review of "Endocrinology of Social Relationships"

P. Ellison and P. Gray. Cambridge, MA: Harvard University Press, (512 pp. Price: $49.95)

In chess, a gambit is the sacrifice of material, usually pawns, in order to gain superior position. In evolutionary biology, the "phenotypic gambit" is the implicit assumption that genetic data can be sacrificed in testing evolutionary hypotheses because phenotypes adequately predict underlying genotypes (Grafen, 1984). Evolutionary psychologists often play a third gambit, which I will call the psychologic gambit. This is the implicit assumption that neurophysiological underpinnings can largely be ignored when testing evolutionary hypotheses about behavior and psychology. After all, if one is interested in the evolutionary functions of behavioral and psychological patterns, does it matter whether these patterns depend upon the nucleus accumbens or the basolateral amygdala, for example, or upon vasopressin or oxytocin, when selection really only "sees" the behavior? Thus, although Tooby and Cosmides (2005, p. 6) note that evolutionary psychological models should eventually "include the neural, developmental and genetic bases" of psychological mechanisms, evolutionary psychologists in general do not appear to view this need as pressing.

On the one hand, the psychologic gambit has profitably directed research in evolution and behavior. We have made considerable progress in understanding the evolutionary functions of mate preferences, for example, without knowing the neurophysiological bases of these preferences. On the other hand, more detailed proximate knowledge better characterizes the phenotype to be explained and can thus clarify ultimate causes. For example, the functional reasons for menstrual cycle variation in women's mate preferences (Gangestad & Thornhill, 2008) will likely be elucidated by knowledge of its hormonal basis. Hormonal data have been used to test whether cyclic preference shifts function in recruiting high-quality genes near ovulation or are byproducts of a pregnancy-related adaptation or an adaptation for changing preferences between cycles (Jones et al., 2005; Puts, 2006; Roney & Simmons, 2008).

Of course, ultimate understanding can also clarify proximate mechanisms such as hormone-behavior relationships. Consider the debate about whether androgens have "activational" effects (disappearing after the hormones leave the blood) or only "organizational" (relatively permanent) effects on human spatial cognition (Puts, Gaulin, & Breedlove, 2007). This debate may be informed by the hypothesis that male ranging behavior and spatial ability function in mate location (Gaulin & FitzGerald, 1986). In seasonally breeding rodents, male testosterone levels, range size and navigational ability increase during the breeding season (Galea, Kavaliers, & Ossenkopp, 1996; Gaulin & FitzGerald, 1989), whereas androgens have only organizational effects on spatial navigation in non-seasonal breeders (Commins, 1932). Seemingly, selection tends to favor continued androgen responsiveness of costly ranging behaviors and their neurophysiological substrates in seasonally breeding species. This functional insight suggests that androgens might not have activational effects on spatial ability in a largely non-seasonally breeding species such as humans.

In their edited volume *Endocrinology of Social Relationships* (*ESR*), Peter Ellison and Peter Gray recognize that ultimate and proximate (perhaps especially neuroendocrine) explanations make reciprocal contributions, and emphasize the importance of approaching behavioral questions from all levels of Tinbergen's (1958) fourfold explanatory framework. *ESR* is a collection of 16 well-written reviews, by authorities in their respective areas, of the roles played by hormones in mediating social relationships, including parental care, mating behavior, and dominance. Ellison and Gray are themselves "heavy hitters" in behavioral endocrinology, and so it is unsurprising that they were able to recruit many of the stars of the field to author chapters. Part 1 of the book's three sections provides theoretical and empirical background in evolution and behavioral endocrinology. Although *ESR* highlights human research, Part 2 focuses on social relationships among nonhuman mammals, and Part 3 focuses on the endocrinology of human social relationships.

The chapters of *ESR* generally do an excellent job of illustrating the interrelatedness between explanations at multiple levels. For example, in chapter 3, Peter Ellison discusses how hormones carry information about the state of the organism, facilitating adaptive allocation of reproductive effort in response to this information, and Emery Thompson's chapter on the endocrinology of social relationships in nonhuman apes is pleasantly infused with much ultimate-level explanation. Pablo Nepomnaschy and Mark Flinn review how children's stress responses are influenced by early life events, adeptly integrating proximate and ultimate levels of analysis in suggesting that responses to stress (e.g., depression) may be adaptations and that apparent negative outcomes may have unknown benefits to survival and reproduction.